

BODY CONDITION AND MATE CHOICE IN *TETRAGNATHA ELONGATA* (ARANEAE, TETRAGNATHIDAE)

Anne Danielson-François¹: Dept. of Biology, Swarthmore College, Swarthmore, PA 19081. E-mail: adaniels@u.arizona.edu

Christine A. Fetterer and Peter D. Smallwood: Dept. of Biology, University of Richmond, Richmond, VA 23173

ABSTRACT. The mate preference characteristics of adult *Tetragnatha elongata* were assessed with respect to measures of female mass, linear size (length), and condition (mass scaled by length: body condition). Males preferred longer, heavier females and females with higher body condition indices. When mass is partially controlled, males still preferred females of higher body condition, but reversed their preference for length and chose smaller females. We present evidence that female body condition and mass are associated with the volume of her egg load and the proximity of oviposition, whereas female body length is not associated with either. Females displayed no clear preference among males for mass or linear size, but were reluctant to mate in female-choice trials. The small sample size obtained may have obscured the detection of female mate preferences if they exist. This may be the first evidence that mate choice is influenced by body condition rather than mass or linear size among spiders.

Keywords: Mate choice, size, body condition, oviposition, *Tetragnatha elongata*

Body size is a signal used by many animals to assess the quality of a mate. Measurements of mate quality, including overall energy intake, genetic quality, and other components of fitness, are associated with larger body size in both sexes (Andersson 1994). Larger males often achieve higher mating success by winning competitions for mates or through pre- or post-copulatory mate guarding (Parker 1970). Females may benefit by choosing larger males because these males have higher lifetime mating success, higher genetic quality or more vigorous copulatory courtship (Eberhard 1991, 1996). Males may benefit by choosing larger females when larger females have higher quality offspring or greater fecundity (Andersson 1994).

For spider species, reproductive success for both sexes also seems to be influenced by body size (as measured by linear dimensions) and mass. Male body size has been associated with higher reproductive success in several spider species via larger males winning competitions for mates (Riechert 1978; Christenson & Goist 1979; Vollrath 1980; Austad

1983; Rubenstein 1987; Watson 1990; Hack et al. 1997). If this pattern holds true, where mate competition exists females should prefer larger males as mates when given a choice. Similarly, males should prefer heavier females as mates when female fecundity is associated with body mass. Female body mass has been associated with higher fecundity in spiders (Wise 1979; Briceño 1987; Vollrath 1987; Morse 1988; Uetz 1992; Head 1995) and other arthropods (Honek 1993; Spence et al. 1996). Males may also prefer heavier females because their greater mass may indicate that they are closer to oviposition. Mating with females immediately prior to oviposition may give males a reproductive advantage in species with sperm mixing or last-male sperm precedence (Parker 1970; Waage 1979; Miller 1984; Siva-Jothy & Tsubaki 1989; Parker & Simmons 1991; Birkhead & Moller 1998). Last-male sperm precedence is predicted for the orb-weaving spider, *Tetragnatha elongata* Walckenaer 1805 based on female reproductive morphology (Austad 1984; West & Toft 1999). Regardless of sperm precedence, mating closer to oviposition might also reduce the likelihood that a male will lose his gametic investment due to female mortality before oviposition.

¹ Current Address: Dept. of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721.

Recently, it has been argued that body condition is a better estimate of an animal's physiological state (and by extension, its fitness) than either linear size or mass (Jakob et al. 1996 and references therein). Body condition indices are a function of the mass of the animal, adjusted for its linear size, and may be particularly useful in measuring female spiders, as they cyclically mature and oviposit their eggs. While the female's linear size remains constant, her mass and body condition vary considerably over the course of this cycle, as her unsclerotized abdomen expands or contracts with feeding and starvation, yolk deposition or oviposition. Jakob et al. (1996) evaluated three different body condition indices using two spider species. They found that a condition index based on the residual index performed the best, and had the most straightforward biological interpretation (see Kotiaho 1999; Marshall et al. 1999 for further discussion). However, we are not aware of data to support the hypothesis that body condition *per se* (c.f., mass) correlates with fecundity in female spiders or with the timing of oviposition. It is also not known if body condition directly influences mate choice (independent of mass and/or linear size).

Here we examine the influence of linear size, mass, and body condition on mate choice in *T. elongata*. We also examine oviposition in female *T. elongata* to see how linear size, mass, and body condition correlate with measures of fecundity and the timing of oviposition.

METHODS

Natural history and collection.—Little is known about the natural history and mating behavior of *T. elongata* (Levi 1981; Gillespie 1987; Smallwood 1993). Individuals build orb webs over or near water throughout the eastern and southern United States (Levi 1981). They typically rebuild their webs daily and, in some circumstances, relocate almost as often (Gillespie & Caraco 1987; Smallwood 1993). Individuals exhibit aggregative behavior at high prey densities and often share silk lines, although not prey, in these groups (Gillespie 1987). They are nocturnally active spiders. During daylight hours, females rest beside their webs while adult males often move between aggregations of females (Danielson-François, pers. obs.). Both adult males and fe-

males live for several months and mate repeatedly. Females lay multiple egg sacs beginning two weeks after the final molt and continuing until death (Danielson-François, pers. obs.). Several generations may overlap during the warmer months.

The 105 adult *T. elongata* for the initial mating study and the oviposition study were collected along the banks of the Crum Creek in eastern Pennsylvania, Delaware County (39°37' N; 75°7' W) from June to September 1993 and 1994. An additional 144 adults were collected from the banks of Westhampton Lake in Richmond, Virginia (32°30' N; 77°32' W) from June to September 1998. These spiders were used to continue mating studies. The study sites were repeatedly sampled for spiders and as new adults matured they were collected. However, given the high frequency of mating these adults were unlikely to be virgins and, after collection, several females laid egg sacs that later hatched. While it would be ideal to use virgins in the study, at least in *T. elongata*, males and females do mate multiple times and males reinduct sperm (Danielson-François, pers. obs.). Separate sets of animals were used in the mating and oviposition studies.

Individual spiders were marked with bands of Testor's model paint and housed in clear acrylic aquaria (ranging from 40 L × 20 W × 15 H to 100 × 50 × 62 cm). Spiders were fed *ad libitum* (*Drosophila* spp. and Tipulidae spp.) for the mate choice study and for the oviposition study were kept on a standardized diet (eight *D. virilis* daily). Voucher specimens for the study are deposited in the collection curated by the Department of Entomology, University of Arizona, Tucson, Arizona, USA.

Linear size, mass and condition.—We measured the right femur of the first leg to the nearest 0.1 mm (as a measure of linear size) and weighed each adult collected to the nearest 0.001 g. We assigned each female a body condition score (BCS hereafter) by generating a residual index. The residual index was constructed by regressing log-transformed mass against log-transformed femur length following the methods of Jakob et al. (1996). BCS for an individual spider is its residual (positive or negative) from the regression. Residuals were analyzed and variance in the index was homogeneous across different linear sizes as

determined by visual inspection. Females with higher BCS are heavier for their linear size.

Mate choice trials.—Male preferences were assessed by introducing a male into an aquarium with two females of significantly different linear size and mass and observing his behavior. Collected females were divided visually into large and small linear size classes. The spiders were kept on a 12:12 light-dark cycle at room temperature. We conducted mate choice trials between 13:00–16:00 (dark period of the cycle) and observed the spiders under a dim red light.

We recorded both body length and mass for both female spiders in each trial. The longer females had significantly longer femurs than small females ($n = 78$, $\bar{x} = 12.90 \pm 0.13$ mm, $\bar{x} = 11.20 \pm 0.16$ mm, respectively; paired t-test; $t = 12.0$, $df = 77$, $P < 0.0001$). Heavier females weighed significantly more than lighter females ($n = 78$, $\bar{x} = 0.066 \pm 0.002$ g, $\bar{x} = 0.045 \pm 0.001$ g, respectively; paired t-test; $t = 13.7$, $df = 77$, $P < 0.0001$).

Each test pair of females was introduced into the tank at least one day before the trial to allow females to adjust to the tank and to spin a web. Some tanks had a partial partition dividing the tank into two halves, and all tanks were large enough for each female to build her own (albeit small) web. Males were placed between the females' webs. We recorded the linear size of female chosen (roughly, large or small) and the duration of the mating. If a male mated with both females, the order in which he copulated also was recorded. As males usually attempted to mate within minutes of being placed in aquaria, the trial was terminated if the male remained stationary and did not copulate within 1 h. Usually, males that did not mate wandered for a few minutes and then remained stationary and did not roam or contact the web strands.

Many spiders were used in more than one trial, but each trial was unique. No male was used more than 3 times, no pair of females was used more than twice, and no pair was ever tried against the same male more than once. A total of 93 males and 156 females were used in the mating trials.

Likewise, presenting a female with two males of significantly different linear sizes assessed female preferences. Males were separated into large and small linear size classes upon collection. Large males were signifi-

cantly longer than small males in femur length ($n = 11$, $\bar{x} = 0.06 \pm 0.02$ mm, $\bar{x} = 0.02 \pm 0.01$ mm, respectively; paired t-test; $t = 5.27$, $df = 10$, $P = 0.0004$). Heavy males weighed significantly more than lighter males ($n = 11$, $\bar{x} = 0.06 \pm 0.02$ g, $\bar{x} = 0.02 \pm 0.01$ g, respectively; paired t-test; $t = 4.97$, $df = 10$, $P = 0.0006$). Each female was placed in an aquarium and allowed to adjust to her enclosure and spin a web at least a day before the males were introduced. Two males were simultaneously placed on opposite sides of her web. Female choice was determined by observing until the female copulated with one of the males, or for one hour at which point the trial was terminated.

Oviposition.—Female *T. elongata* lay egg sacs continuously from two weeks after the final molt until death and are receptive to re-mating at any time, even the day before laying eggs. We predict that males will prefer heavier females, or those of higher body condition. This prediction is based on the assumption that such females are more fecund or closer to oviposition. Therefore, we tested female mass for an association with the timing of oviposition, the number of egg sacs laid, and a volumetric measure of the number of eggs in each sac. A separate group of 26 females was collected for studies involving the volume of the egg mass, while other analyses included females used in the mate choice trials. These females were fed a standard diet (eight *D. virilis* daily) which allowed them to gain weight slowly during the study. While each female was being weighed, her aquarium was checked for egg sacs. We recorded the number of egg sacs and the date laid for each female until she died.

Individual eggs were agglutinated and thus could not be counted; however, because the eggs were tightly packed together, we used the volume of the egg cluster the day it was laid as a measure of maternal investment. The volume of the egg cluster was calculated from the length, width, and height of the agglutinated eggs after the egg sac was stripped of silk. We examined the association between the volume of the egg cluster and the mass of the female from five days to one day before oviposition.

Statistical analyses.—For the mate choice trials, a binomial probability test was used ($p = q = 0.5$) with equal probability of mating

or not mating (Sokal & Rohlf 1995). Pairs of females or males used in mate choice trials were tested for significant differences in linear size using Student's paired t-test. ANOVA and simple linear regression were used to test for associations between female mass, egg cluster volume and number of days until next oviposition. All summary statistics of continuous variables are reported as $\bar{x} \pm \text{SE}$.

RESULTS

Mating behavior.—Overt courtship in *T. elongata* appeared very subtle or non-existent, contrary to that seen in most orb-weaving spiders (LeSar & Unzicker 1978; Robinson & Robinson 1980; Robinson 1982). Males positioned themselves at the edge of a female's web and made slight leg movements on the strands of the web. They often tapped the silk for a few seconds, paused with their first pair of legs resting gently on the web strand, then repeated the behavior until the female responded. Females almost instantly oriented to the male's vibrations and vibrated the web in response.

The vibrations of the female were either fast arrhythmic pulses or slower rhythmic pulses and seemed to predict her response to the male. When a female exhibited vigorous arrhythmic pulses, males approaching any further onto the web were chased away. Similar arrhythmic web vibrations were observed from a female as large prey became entangled in her web, prior to her attack on the prey. Only when the female pulsed rhythmically could the male approach her without interference. In the field, males would sometimes steal prey from female webs when the female exhibited slow rhythmic vibrations. More often, once a male made this initial contact with an accepting female, they paired immediately. As the male approached, both sexes spread their chelicerae and fangs apart. Within seconds the pair then vigorously grappled to interlock cheliceral fangs and assumed a ventral-to-ventral position for mating. The male used his 3rd pair of legs to contact the female's abdomen and often moved her into position, sometimes even shaking her until he successfully inserted his pedipalp.

Mating duration varied ($n = 77$, $\bar{x} = 416 \pm 31$ seconds). Once chelicerae were engaged, mating consisted of several alternating insertions of each pedipalp and was terminated by

cheliceral disengagement. During each insertion, the male inflated the hematodochae of his pedipalp repeatedly.

Females appeared to terminate matings. These terminations often occurred when the male was in the process of switching from one pedipalp to another. The female pressed her chelicerae together, bringing her fangs closer to the body of the male. The male used his 3rd pair of legs to press his body away from the female as she moved her chelicerae. Once the chelicerae were disengaged, the male quickly retreated from the web, while the female would remain where she had been mated. Sometimes, after mating, the female chased the male a short distance with her chelicerae and fangs spread open before returning to her former position. Occasionally, males were cannibalized after mating.

Linear size and mass.—Overall, females ranged in mass from 0.02–0.11 g ($n = 156$, $\bar{x} = 0.056 \pm 0.001$ g), and were significantly heavier than males who ranged from 0.01 to 0.08 g ($n = 93$, $\bar{x} = 0.034 \pm 0.001$ g) in mass ($df = 247$, unpaired $t = 11.67$, $P \leq 0.0001$). Males ranged in femur length from 6.95–20.0 mm ($n = 93$, $\bar{x} = 12.47 \pm 0.18$ mm), while females exhibited a significantly smaller range from 7.0 to 15.1 mm ($n = 156$, $\bar{x} = 12.05 \pm 0.12$ mm) in femur length (unpaired $t = -1.99$, $df = 247$, $P = 0.048$). Both male femur length and mass ($r^2 = 0.27$, $F_{1,90} = 32.6$, $P \leq 0.0001$; Fig. 1) and female femur length and mass had a significant positive association ($r^2 = 0.45$, $F_{1,154} = 126.2$, $P \leq 0.0001$; Fig. 1).

Characteristics of mate preference.—We conducted 107 trials in which males were presented with a choice between two females. Mating occurred in 78 trials, usually within a few minutes. In unsuccessful trials, males did not seek females but instead remained stationary for one hour, after which the trial was ended.

Males showed a significant preference for females based on their mass, linear size, and BCS (Table 1). Mass, linear size, and BCS are related. In an attempt to tease apart the effects of each, we examined a subset of trials, those where the mass difference between the females was less than 20%. We chose the 20% cutoff in an effort to minimize the effects of mass, while still leaving a useful sample size. For the female pairs with less than 20% dif-

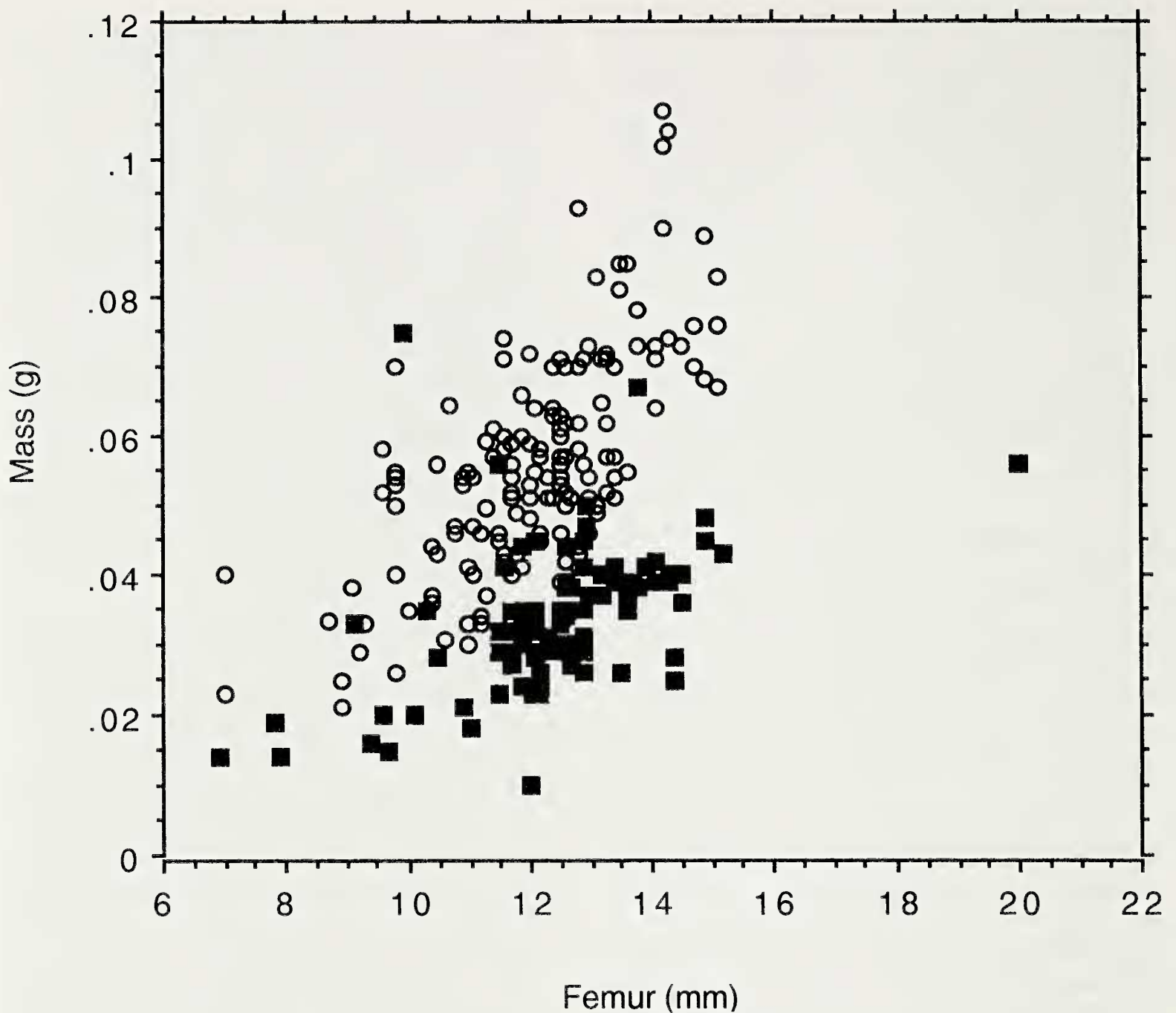


Figure 1.—Relationship between *T. elongata* mass and femur length of both females (open circles, $n = 156$) and males (filled squares, $n = 93$).

ference in mass, males exhibited no preference for heavier or lighter females. With mass partly controlled, males showed no preference for females based on their linear size. In fact, males preferred females of smaller linear size over longer females (Binomial test, $P = 0.0327$, Table 1). Smaller females of nearly the same mass are necessarily heavier in proportion to their linear size—in other words, they have a higher BCS. With the variation in mass minimized (less than 20% difference), males exhibited a significant preference for females of higher body condition (Binomial test, $P = 0.0328$, Table 1). We were not able to conduct a similar analysis minimizing variation in body condition, because there were only 3 cases where BCS differed by less than 20%.

Mated females had significantly higher body condition indices than unmated females ($n = 78$, $\bar{x} = 0.055 \pm 0.021$, $\bar{x} = -0.055 \pm 0.026$, respectively; ANOVA, $F_{1,154} = 10.85$, $P = 0.0012$). The variance of the residuals (the body condition scores) was homogeneous across different linear sizes as determined by visual inspection of the graphed residuals.

For the female mate preference trials, 18 females were presented with two males and mating occurred in 12/51 trials. Females showed no deviation from random mating with respect to male length or mass (Table 1) in the successful trials. Several females of large linear size did vigorously chase after mates with their chelicerae spread once mating ended. Cannibalism occurred in two trials in which two such females, who had indicated

Table 1.—Body characteristics and mate preference (binomial test, where $p = q = 0.5$).

Male mate preference			
Female characteristics		Mated females (<i>n</i>)	<i>P</i>
All trials			
Mass:	Heavier	45	0.0002
	Lighter	14	
Linear Size:	Larger	43*	<0.0001
	Smaller	13	
Body Condition:	Higher	42	0.0005
	Lower	17	
Trials in which mass differed by <20%			
Mass:	Heavier	10	0.176
	Lighter	9	
Linear Size:	Larger	5	0.0327
	Smaller	13	
Body Condition:	Higher	12	0.0328
	Lower	7	
Female mate preference			
Male characteristics		Mated Males (<i>n</i>)	<i>P</i>
Mass	Heavier	5	0.22
	Lighter	3	
Linear Size:	Larger	8	0.12
	Smaller	4	

sexual receptivity, consumed their mates immediately following mating and cheliceral disengagement.

Oviposition.—Of the 26 females used in the study of egg mass, 18 laid egg sacs for a total of 52 sacs. These 18 females laid between one and seven egg sacs ($\bar{x} = 2.7 \pm 0.4$ sacs). The egg sacs did not change significantly in volume as a function of whether they were the first ($\bar{x} = 0.051 \pm 0.009 \text{ cm}^3$), second ($\bar{x} = 0.031 \pm 0.006 \text{ cm}^3$); third ($\bar{x} = 0.026 \pm 0.004 \text{ cm}^3$) or fourth ($\bar{x} = 0.048 \pm 0.031 \text{ cm}^3$) sacs measured (first-second, unpaired t-test, $t = 1.124$, $df = 25$, $P = 0.27$; second-third, paired t-test $t = -0.50$, $df = 7$, $P = 0.63$; third-fourth, paired t-test, $t = -0.99$, $df = 2$, $P = 0.42$). The number of days between the first and second egg sacs ($\bar{x} = 10 \pm 1.2$; $n = 15$, range 4–20 days), compared to the number of days between the second and third sacs ($\bar{x} = 7 \pm 1$; $n = 8$, range 2–10 days), did not significantly differ (unpaired t; $t = 1.81$, $df = 21$, $P = 0.084$). We were not able to test the

Table 2.—Regression of parameters of fecundity on female characteristics.

Female characteristic	<i>n</i>	r^2	<i>P</i>
Volume of first egg cluster			
Mass (day prior)	17	0.270	0.032
Linear Size	17	0.005	0.79
Body Condition	17	0.231	0.051
Summed volume of first and second egg clusters			
Mass (day prior)	15	0.278	0.003
Linear Size	15	0.018	0.48
Body Condition	15	0.321	0.0011
Summed volume of all egg clusters			
Mass (day prior)	17	0.119	0.18
Linear Size	17	0.001	0.89
Body Condition	17	0.205	0.068
Number of egg cases (two or more) produced			
Mass (initial)	15	0.079	0.31
Linear Size	15	0.024	0.58
Body Condition	15	0.058	0.39
Total number of egg cases produced			
Mass (initial)	18	0.048	0.38
Linear Size	18	0.052	0.36
Body Condition	18	0.025	0.53
Days to oviposition			
Mass (initial)	18	0.187	0.073
Linear Size	18	0.136	0.13
Body Condition	18	0.015	0.63

differences with the number of days between the third and fourth sacs ($\bar{x} = 9 \pm 6$; $n = 4$, range 5–17 days) and the number of days in between the fifth, sixth and seventh egg sacs (range 3–6 days) because the small sample sizes precluded any further analyses.

We used simple linear regression to examine the relationship between measures of the female body (mass, BCS and linear size) and measures of her fecundity, the volume of the egg cluster laid and the number of egg sacs produced (Table 2). Egg cluster volume was associated with female mass and BCS, while linear size was not. Significant relationships were found between female mass (prior to egg-laying) and the volume of the first egg cluster laid, as well as the summed volume of the first two egg clusters. Significant relationships were also found between female BCS and the summed volume of the first two egg clusters. Female linear size was not significantly associated with any measures of the volume of the egg clusters. Neither female

Table 3.—Female body characteristics on days prior and post oviposition.

Female characteristic	$\bar{x} \pm \text{SE}$ prior	$\bar{x} \pm \text{SE}$ post	<i>n</i>	<i>F</i>	<i>P</i>
Mass (1 d prior: 1 d post)	0.073 \pm 0.006	0.046 \pm 0.003	21	16.7	0.0002
Mass (1 d prior: 4 d prior)	0.059 \pm 0.005	0.051 \pm 0.004	16	1.62	0.21
BCS (1 d prior: 1 d post)	0.226 \pm 0.039	-0.226 \pm 0.062	21	38.1	<0.0001
BCS (1 d prior: 4 d prior)	0.179 \pm 0.053	-0.179 \pm 0.044	16	5.22	0.0295

Linear Size (No comparison: does not change in individual adult spiders).

mass, linear size nor BCS were associated with the total number of egg sacs produced.

Simple linear regression did not detect a significant relationship between mass, BCS or linear size and days to oviposition (Table 2). However, BCS and mass were significantly higher for females the day prior to oviposition than for females the day after oviposition (Table 3). BCS were significantly higher for females one versus four days prior to oviposition as well, yet this relationship was not seen with female mass (Table 3). We did not test linear size against the timing of oviposition, since an individual spider's linear size remains constant after its final molt as well as pre- and post-oviposition.

DISCUSSION

We examined three parameters of the female physique for their effect on male choice: mass, linear size, and body condition. Males overwhelmingly chose females who were heavier, longer, and had higher BCS. However, these three parameters were correlated, making it difficult to isolate the parameter(s) determining male choice. By looking at a subset of trials in which variation in female mass was partly controlled (less than 20% difference), we were able to separate linear size from the other two parameters. With the influence of mass minimized, males exhibited a significant preference for females with higher BCS, who *ipso facto* were the smaller females in these trials. Thus, we have shown that male choice is influenced by body condition, independent of mass and linear size. Our data set does not allow us to test mass in a similar fashion. Mass may have a similar independent effect on male choice, or it may merely be correlated with body condition. Female linear size, however, does not appear to influence male choice: it is merely correlated with mass and body condition.

Possible explanations for male preferences

are that they result in mating with females (1) carrying heavier egg loads, or (2) closer to oviposition. It is possible that male preferences could be influenced by other components of fitness such as increased egg size (but see Anderson 1990) or higher genetic quality, but these were not tested in this study. And we note that these hypotheses are not mutually exclusive.

The first hypothesis, that male preferences are influenced by egg load, has some support from our data. Female mass explained 12–28% of the variation in egg cluster volume, an estimate of egg load. Female body condition explains 21–32% of this variation. It appears that female mass and/or body condition may account for variation in the egg load a female is currently maturing but does not entirely predict her future success. Neither female mass nor body condition predicts the number of future egg sacs. However, variation in body condition explained 21% of variation in the summed volume of future egg sacs in our study. Several authors have reported relationships within orb-weaving species between increased female mass and increased egg load in spiders (Wise 1975, 1979; Morse 1988) and comparative studies across many species reveal selection for increased female linear size through fecundity selection (Head 1995; Prenter et al. 1999). Glazier (2000) reports positive associations between body condition and brood mass in amphipods, but we are not aware of any empirical evidence that body condition is positively associated with egg load in spiders.

The second hypothesis, that male preferences are influenced by proximity to oviposition, is somewhat supported by our data. Females do have significantly higher mass and body condition indices on the day of oviposition than at other times (the day after or 4 days prior). While the trend appeared to be in

the expected direction, we were unable to detect a significant relationship between female mass or body condition and overall time to oviposition. A partial explanation for this result may be that females gain mass rapidly just prior to oviposition. In *T. elongata*, the day before oviposition, females can gain weight in excess of 30% of their total body mass, all in one 24 hour period. As female spiders gain weight before oviposition, their abdomens swell with mature eggs. In an interesting twist, Funk and Tallamy (2000) found that females of the long-tailed dance fly deceive mate-seeking males with an unreliable signal that eggs are nearing maturation by inflating their abdomens (via swallowing air) in order to gain a protein meal in exchange for copulation.

Future studies to separate the effects of mass and body condition would be most helpful here. Several have argued that body condition is a better measure of fitness than mass (e.g., Jakob et al 1996; Glazier 2000), but data linking body condition to oviposition in spiders have yet to be reported. Both mass and body condition correlate with some measures of fecundity in our study, but our data set does not allow us to separate the effects of mass from those of body condition. The two parameters may be complementary.

In contrast to BCS and mass, we found no evidence of male preference for longer females, nor any relationship between female linear size and any parameters of fecundity or oviposition. There are several possible explanations for the lack of male response to longer females: (1) under lab conditions longer females are not much heavier than gravid small females, (2) female-female competition for high quality web sites favors longer females and leads to better foraging, and (3) mass is easier than linear size for males to assess from the edge of an orb web. These are discussed in turn below.

That female linear size would not influence egg load or the number or volume of future egg sacs is contrary to other fecundity studies of spiders (Marshall & Gittleman 1994; Head 1995; Prenter et al. 1999). However, in a more natural setting, female linear size could be strongly associated with feeding and egg sac production in *T. elongata*. All spiders in our egg sac study were fed the same amount of food to allow for controlled comparisons. In

the field, longer females may build larger webs or use higher-quality web sites to capture more food than smaller females. Female spiders tend to be food-limited (Wise 1975, 1979) so increased energy intake may allow for larger egg sacs, shorter intervals between egg sacs or increased longevity resulting in more egg sacs. Spence et al. (1996) found no relationship between linear size and reproductive output in the nursery web spider *Dolomedes triton* (Walckenaer 1837) when food availability was low. However, when more food was available than actually consumed, the reproductive output of larger females was significantly greater than that of smaller females. In our study, the lack of an effect of linear size may result from longer females being food-limited by access to smaller prey (Tipulidae and *D. virilis*) than the females would catch naturally, such as damselflies (Zygoptera) and moths (Danielson-François, pers. obs.).

Longer females may be heavier in the field as the result of better foraging from high quality web sites. There is competition for these high quality web sites from other females who invade each other's webs in aggressive interactions (Smallwood 1993). Sometimes these interactions result in the web owner losing her web to the intruder, and occasionally in a spider being killed and cannibalized (Smallwood 1993). If longer females are more likely to win in aggressive encounters (Rubenstein 1987), greater linear size may increase female fitness by reducing the probability that she loses her web site (which would interrupt her feeding), or is killed before depositing her eggs. These fitness consequences would not be detected by our measurement of egg production under controlled laboratory conditions.

Mass may be easier to assess than linear size in orb-weaving spiders, which have notoriously poor vision yet are able to accurately assess the mass of objects in their webs via vibrations (Suter 1978; Foelix 1996). In assessing a potential mate from a distance (at the edge of a web), mass may simply have been easier for males to assess or a more relevant cue than length for mate quality. For *T. elongata*, mating is guaranteed once the female in her web orients to the male on the web edge and both open their chelicerae (at a distance of 10 cm or more) and the male

speedily approaches to lock her chelicerae open. By the time both parties are within their range of vision, the decision to mate is a *fait accompli*.

We detected no clear patterns to female choice, but a high proportion of trials, 39 out of 51, did not result in any mating. The resulting small sample size may have prevented us from detecting any female preferences. It is also possible that the simultaneous proximity of two males disrupted the normal behaviors of the female as a fair number deserted their webs. It was rare for us to observe more than one male interacting with a female or her web in the field. Alternatively, male-male competition for access to females might normally prevent females from encountering a range of male linear sizes. Two of us (ADF, PDS) have seen direct evidence of male-male competition in the field: two males fighting directly adjacent to a female's web. The winner of the contest mated with the female immediately afterwards. Future experiments to determine whether the female is actually choosing or merely accepting winners are needed. Female preference may be difficult to detect because females may be choosing males post-mating via cryptic female choice (Eberhard 1994, 1996). Cannibalism may be the end result of a female preference, yet it was an infrequent occurrence (occurred in two mating trials). While our limited data support that smaller males are more likely to be cannibalized (Elgar & Nash 1988), female hunger level may be a better predictor (Andrade 1996).

The mating history of males and females was unknown because they were collected as adults. Our study assumes that the mating history of females was random relative to female length and mass so our conclusions regarding male choice should hold. In this species, past mating history may not have as significant influence on male mate choice as expected for most spiders because female *T. elongata* are predicted to have last-male sperm precedence, continually deposit egg sacs at regular intervals and continue to be receptive to further mating.

As far as we know, this is the first report of body condition influencing mate choice in spiders. Taylor et al. (2000) suggest that the display used by the salticid *Plexippus paykulli* (Audouin 1826) is designed to convey infor-

mation about body condition to potential mates and rivals. Salticids are known for their visual acuity. It is not clear how male *T. elongata* would sense body condition in nearby females unless length and mass are separate components of a vibratory signal transmitted through the web. It may be that there is some other signal (e.g., pheromone) that correlates with an important parameter of female fecundity, which is also correlated with body condition.

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LITERATURE CITED

- Andrade, M. 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science* 271:70-72.
- Anderson, J.F. 1990. The size of spider eggs and estimates of their energy content. *Journal of Arachnology* 18(1):73-78.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey.
- Austad, S. 1983. A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Animal Behaviour* 31: 59-73.
- Austad, S. 1984. Evolution of sperm priority patterns in spiders. Pp. 223-249, *In* Sperm Competition and the Evolution of Animal Mating Systems (R. L. Smith, ed.). Academic Press, Orlando, Florida.
- Birkhead, T. & A. Moller. 1998. *Sperm Competition and Sexual Selection*. Academic Press, San Diego, California.

- Briceño, R. 1987. How spiders determine clutch size. *Revista de Biología Tropical* 35:25–29.
- Christenson, T.E. & K.C. Goist. 1979. Costs and benefits of male-male competition in the orb-weaving spider *Nephila clavipes*. *Behavioral Ecology & Sociobiology* 5:87–92.
- Eberhard, W.G. 1991. Copulatory courtship and cryptic female choice in insects. *Biological Reviews* 66:1–31.
- Eberhard, W.G. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. *Evolution* 48:711–733.
- Eberhard, W.G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton, New Jersey.
- Elgar, M. & D. Nash. 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour* 36:1151–1157.
- Foelix, R. 1996. *The Biology of Spiders*. Second Edition. Oxford University Press: New York, New York.
- Funk, D.H. & D.W. Tallamy. 2000. Courtship role reversal and deceptive signals in the long-tailed dance fly, *Rhamphomyia longicauda*. *Animal Behaviour* 59:411–421.
- Glazier, D.S. 2000. Is fatter fitter? Body storage and reproduction in ten populations of the freshwater amphipod *Gammarus minus*. *Oecologia* 122:335–345.
- Gillespie, R.G. 1987. The role of prey availability in aggregative behavior of the orb weaving spider *Tetragnatha elongata*. *Animal Behaviour* 35:675–681.
- Gillespie, R.G. & T. Caraco. 1987. Risk-sensitive foraging strategies of two spider populations. *Ecology* 68:887–899.
- Hack, M.A., Thompson, D.J. & D.M. Fernandes. 1997. Fighting in males of the autumn spider, *Metellina segmentata*: Effects of relative body size, prior residency and female value on contest outcome and duration. *Ethology* 103:488–498.
- Head, G. 1995. Selection on size and fecundity and variation in the degree of sexual size dimorphism among spider species. *Evolution* 49:776–782.
- Honek, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66:483–492.
- Jakob, E.M., Marshall, S.D., & G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77(1):61–67.
- Kotiaho J.S. 1999. Estimating fitness: comparison of body condition indices revisited. *Oikos* 87:399–400.
- LeSar, C. & J. Unzicker. 1978. Life history, habits and prey preferences of *Tetragnatha laboriosa* (Araneae: Tetragnathidae). *Environmental Entomology* 7:879–884.
- Levi, H.W. 1981. The American orb-weaver genera *Dolichognatha* and *Tetragnatha* North of Mexico (Araneae: Araneidae, Tetragnathinae). *Bulletin of the Museum of Comparative Zoology* 149(5):271–318.
- Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? *Functional Ecology* 8:118–124.
- Marshall, S.D., Barrow, J.H., Jakob, E.M. & G.W. Uetz. 1999. Re-estimating fitness: can scaling issues confound condition indices? *Oikos* 87:401–402.
- Miller, P.L. 1984. The structure of the genitalia and the volumes of sperm stored in male and female *Nesciothemis farinosa* (Foerster) and *Orthetrum chrysostigma* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 13:415–428.
- Morse, D. 1988. Relationship between crab spider *Misumena ratia* nesting success and earlier patch-choice decisions. *Ecology* 69:1970–1973.
- Parker, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* 45:525–567.
- Parker, G.A. & L.W. Simmons. 1991. A model of constant random sperm displacement during mating: evidence from *Scatophaga*. *Proceedings of the Royal Society of London, Series B* 246:107–115.
- Prenter, J., Elwood, R. & I. Montgomery. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution* 53:1987–1994.
- Riechert, S. 1978. Games spiders play: behavioral variability in territorial disputes. *Behavioral Ecology & Sociobiology* 3:135–162.
- Robinson, M. 1982. Courtship and mating behaviour in spiders. *Annual Review of Entomology* 27:1–10.
- Robinson, M. & B. Robinson. 1980. Comparative studies of the courtship and mating behavior of tropical Araneid spiders. *Pacific Insects Monographs* 36:1–218.
- Rubenstein, D.I. 1987. Alternative reproductive tactics in the spider *Meta segmentata*. *Behavioral Ecology & Sociobiology* 20:229–237.
- Siva-Jothy, M.T. & Y. Tsubaki. 1989. Variation in copula duration in *Mnais pruinosa pruinosa* Selys (Odonata: Calopterygidae). *Behavioral Ecology & Sociobiology* 24:39–45.
- Smallwood, P. 1993. Web-site tenure in the long-jawed spider: is it risk-sensitive foraging, or conspecific interactions? *Animal Behaviour* 74:1826–1835.
- Sokal, R.R. & F.J. Rohlf. 1995. *Biometry*. Third Edition. W. H. Freeman & Co., New York.
- Spence, J.R., Zimmermann, M. & J.P. Wojcicki. 1996. Effects of food limitation and sexual cannibalism on reproductive output of the nursery web spider *Dolomedes triton* (Araneae: Pisauridae). *Oikos* 75(3):373–382.

- Suter, R.B. 1978. *Cyclosa turbinata* (Araneae, Araneidae): Prey discrimination via web-borne vibrations. *Behavioral Ecology & Sociobiology* 3: 283–296.
- Taylor, P.W., Hasson, O. & D.L. Clark. 2000. Body postures and patterns as amplifiers of physical condition. *Proceedings of the Royal Society of London Series B* 267(1446):917–922.
- Uetz, G.W. 1992. Foraging strategies of spiders. *Trends in Ecology & Evolution* 7:155–159.
- Waage, J.K. 1979. Adaptive significance of post-copulatory guarding of mates and non-mates by male *Calopteryx maculata* (Odonata). *Behavioral Ecology & Sociobiology* 6:147–154.
- West, H. & S. Toft. 1999. Last-male sperm priority and the mating system of the haplogyne spider *Tetragnatha extensa* (Araneae: Tetragnathidae). *Journal of Insect Behavior* 12(4):433–450.
- Vollrath, F. 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. *Zeitschrift für Tierpsychologie* 53:61–78.
- Vollrath, F. 1987. Growth, foraging, and reproductive success. Pp. 357–370, *In Ecophysiology of Spiders* (W. Nentwig, ed.). Springer, Berlin.
- Watson, P.J. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). *Behavioral Ecology & Sociobiology* 26:77–90.
- Wise, D. 1975. Food limitation of the spider *Linyphia marginata*: experimental field studies. *Ecology* 56:637–646.
- Wise, D. 1979. Effects of an experimental increase in prey abundance on the reproductive rates of two orb weaving spider species (Araneae: Araneidae). *Oecologia* 41:289–300.

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